

## Variation in an Annual Movement Cycle of Flathead Catfish within and between Two Missouri Watersheds

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**Abstract.**—Flathead catfish from the main stems of the Grand River and Cuivre River were implanted with 400-d radio transmitters to determine an annual movement cycle. Substantial variation was observed within and between watersheds. Flathead catfish displayed annual movement that consisted of three main periods punctuated by brief migrations. The first, a period of overwintering was followed by migration from wintering areas in early spring, followed in turn by the prespawn/spawning period, which is characterized by increased activity, including longer movements (up to 187.6 km) during spates. After another short migration period came a third period of postspawn summer/fall restricted movement, which was followed by fall migration back to overwintering areas. Within this framework, individual fish displayed at least three variations of this annual pattern. Some individuals entered Grand River and Cuivre River watersheds during the prespawn/spawning period only, returning to the Missouri River or the Mississippi River during summer/fall, overwintering there, and reentering the tributary the following spring. Other individuals entered tributary watersheds for the prespawn/spawning period and remained there for the summer/fall period, returning to the big rivers to overwinter. In the Grand River, all individuals moved downstream (9–45 km) to the Missouri River and overwintered. Finally, some individuals in Cuivre River remained throughout the year, migrating short distances within the river to spawn, feed, and overwinter. The finding that fish were harvested at locations tens of kilometers from the areas where they spent considerable time suggests a larger scale for management than has previously been proposed.

Restricted movement or nonmigratory behavior has been considered prevalent in stream fishes since the influential writings of Gerking (1950, 1953, 1959). Recently, better methodological treatment of tag-return data and increased life spans of radio transmitters have shown that many species once thought to be strictly residential may, in fact, have fluid population structures; indeed, perhaps most stream fishes make substantial seasonal movements (Lucas and Baras 2001). This “paradigm lost” (Gowan et al. 1994) has forced a reevaluation of the occurrence and seasonality of migrations in species long thought to display restricted movement.

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The flathead catfish *Pylodictis olivaris* has for several decades been considered a species that exhibits restricted-movement behavior (Funk 1957; Robinson 1977; Dames et al. 1989; Skains and Jackson 1995). Although the existence of highly mobile individuals had been observed in studies along the Missouri River in Missouri, the movements were dismissed as irregular and authors continued to suggest that the prevalent condition was that of restricted movement (Grace 1985; Dames et al. 1989). Telemetry studies in two streams in Mississippi, spanning June to the following January, documented limited linear ranges of adult flathead catfish of 1.85 km or less (Skains and Jackson 1995), which suggested that management of riverine populations could be conducted at stream-reach scales as small as 2 km. Drawing largely from these data, Jackson (1999), in a review paper on flathead catfish biology, suggested that locally discrete populations were probable.

In the mid-1990s biologists began to evaluate a population of flathead catfish in the Minnesota

River. Here, near the northern extent of the range of this species, flathead catfish were found to migrate as far as 105 km from summer areas to specific overwintering pools and then return to the summer areas the next year (Stauffer et al. 1996). In 2000, a citizens group seeking the addition of handfishing (noodling) to the legal methods of take in Missouri communicated that adult flathead catfish were predictably present in small tributaries in the northern portion of the state during the spawning season. This information suggested that perhaps the movement patterns of flathead catfish in Missouri were not as restricted as suggested in the literature.

The Missouri Department of Conservation began discussing a statewide catfish management plan in 2001 for waters other than small impoundments—for the first time specifically addressing catfish in rivers and streams (Dames et al. 2003). The feasibility of flathead catfish trophy management areas was seen as an idea that needed local research. The present project was undertaken to provide basic ecological information on the annual movement patterns of adult flathead catfish in interior streams of northern Missouri. Our objectives were to (1) describe the spatial scale at which flathead catfish movements complete an annual cycle and (2) search for patterns of behaviorally defined periods or seasons that might help managers understand the observed movements in a life history context.

### Study Sites

The two study sites chosen were watersheds in northern Missouri without main-stem or major tributary dams that would limit fish movements. The Cuivre River is a seventh-order Mississippi River tributary draining 3,199 km<sup>2</sup> (Figure 1). The channel is characterized by a gravel and sand bottom with scoured pools and sporadic well-defined riffles. The channel exhibits some meandering but also follows valley walls along bluffs, creating long, relatively uniform pools. The Grand River is an eighth-order tributary of the Missouri River, draining 20,461 km<sup>2</sup>. It is characterized by a sinuous channel, meandering lateral pools, and few well-defined riffles. This channel is best described as a regime reach, in contrast to the pool-riffle sequences dominant in the Cuivre River (Montgomery and Buffington 1993). Regime reaches are typical of higher-order rivers flowing in unconstrained valleys. These streams are typified by sand and silt substrates that are constantly in a state of transport, resulting in a bedform regime of ripples,

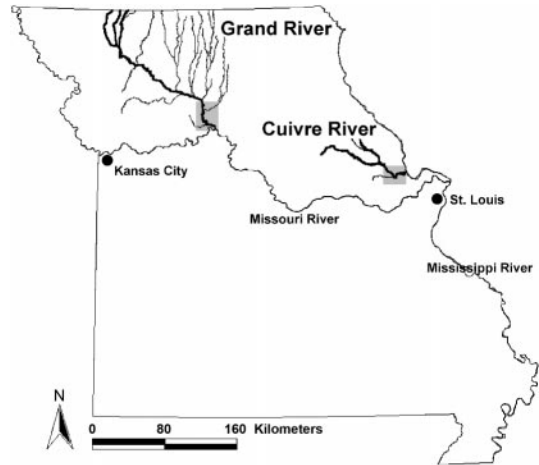


FIGURE 1.—Locations of the Grand River basin and Cuivre River basin (left to right), Missouri. Shaded areas denote the main-stem reaches of the Grand River and the Cuivre River in which flathead catfish were collected and implanted with radio transmitters.

dunes, and antidunes (Knighton 1998). Both streams are within the dissected till plains ecoregion (Hebrank 1989). Historic native vegetation was tallgrass prairie interspersed with patchy woodlands and savanna (Schroeder 1982). The Grand River basin is currently dominated by row-crop agriculture and pasture. The Cuivre River basin is also mostly agricultural but includes a greater portion of large-lot suburban development in the lower basin near St. Louis, Missouri. The Cuivre River basin also includes a portion of the Lincoln Hills region, a karst unglaciated area that historically was forest and still retains a large forest tract at Cuivre River State Park. Large woody debris constituted the dominant structural habitat feature for large fishes in both streams.

### Methods

*Field sampling.*—Flathead catfish were surgically implanted with radio transmitters during June and early July in 2001 in the Grand River ( $N = 37$ ) and in 2002 in the Cuivre River ( $N = 27$ ). Fish were collected by using unbaited hoop nets with front hoop diameters of 60 and 90 cm and bar meshes of 2.54, 3.75, and 5 cm. Hoop nets were set in the lower 50 km of the Cuivre River main stem from its mouth to near Troy, Missouri, and in the lower 61 km of the Grand River main stem from its mouth to near Sumner, Missouri. In an effort to exclude sexually immature juveniles from the study, only fish meeting a minimum size criteria of 51 cm and 1.8 kg were radiotagged (Skains

and Jackson 1995). The fish included for study in the Grand River had a mean total length of 77.8 cm (range, 56.5 to 121.0 cm) and a mean weight of 6.6 kg (range, 1.8 to 21.2 kg). The 27 Cuivre River fish had a mean length of 76.4 cm (range, 55.5 to 113.0 cm) and a mean weight of 6.5 kg (range, 1.9 to 20.9 kg). Fish of this size are presumably 5+ years old (see references in Jackson 1999). Surgeries were conducted on-site and fish were held for a 1-h recovery period in a flow-through pen before release into the same pool from which they had been captured.

The tracking schedule was variable throughout the year because of the weather, the movement rates and dispersal of the fish within the watershed, and the availability of helicopter support. We attempted to locate fish at least weekly (most often twice a week) throughout the entire annual cycle in both basins. Relocations were made during daylight hours by taking two to three bearings and then moving the boat over the signal. In the majority of cases, fish did not move from their location when we approached with the boat. Fish relocations were recorded with global positioning system equipment, differentially corrected with a precision of 0.68–1.4 m. To facilitate other objectives of the research project (see Vokoun 2003), we located fish multiple times throughout the week during the summer and fall. Fish located fewer than 35 times during the annual cycle were removed from calculations describing seasonal movements and ranges.

*Data analyses.*—Distance moved was calculated as a linear distance between successive relocations along a thalweg line created for the main stems of both the Grand River and the Cuivre River. When fish entered tributaries of the main stem of the Grand River or Cuivre River, we estimated distances individually for each such relocation, tracing the tributary channel with digital aerial photographs and the ArcView GIS measuring tool. Using the same process, we calculated distances from relocations to the main-stem river mouth for relocations in the Missouri River and the Mississippi River.

Weekly net movement was defined as the absolute difference along the thalweg line between the most upstream and most downstream relocation for a given week. Weekly net movement values for individual fish were then grouped into months and a mean was calculated for all fish from each river. Monthly means of weekly net movement were combined with the spatial information revealed by the annual tracking to suggest an an-

nual cycle with periods of like movement behavior punctuated by directed migrations through the basin.

The movement patterns could be grouped into three seasonal periods generally corresponding to life history activities demonstrated by all fishes living in temperate streams, namely, reproduction, feeding and growth, and overwintering (Schlosser and Angermeier 1995; Fausch et al. 2002). Using these general sources and the flathead catfish literature (see references in Jackson 1999), we applied descriptive life history activity names to the periods. The range (distance between most upstream and most downstream point) for the three periods of like movement and the overall annual period was calculated. We used two-way analysis of variance (ANOVA) to discern potential differences in range between the three seasonal periods and two rivers. When ANOVA found a difference, we ran Tukey's honestly significant difference test post hoc to determine which class levels of the main effects period and river were significantly different. Data were log-transformed before analysis to achieve normality. A directed movement rate was calculated as the daily distance (km/d) moved by fish during successive relocations that showed directional movement through the watershed. Directed movements as defined here occurred during migration periods and spates.

By examining the relocations spatially in ArcView GIS and plotting the distances from the river mouth against the corresponding calendar dates, we reconstructed the spatial pathways of migration and movement through the two basins. In this description of spatial pathways we included fish that were relocated at least once a month. Several fish were infrequently relocated while they were in the Missouri River or the Mississippi River because of greater attenuation of radio signals associated with the increased depth of the large rivers. We also included locations where anglers harvested radio-tagged fish. If a single fish demonstrated a migration pathway, we have reported it here to highlight the diversity present in the populations in fulfilling the annual cycle. The passive capture method we used to collect fish (hoop nets during the spawn) for radio implantation most likely did not sample the behavioral variations in proportion to their abundance. In fact, by collecting fish only in the main-stem Grand River and the main-stem Cuivre River, we perhaps biased our tagged population toward fish that spawned in the main stems.

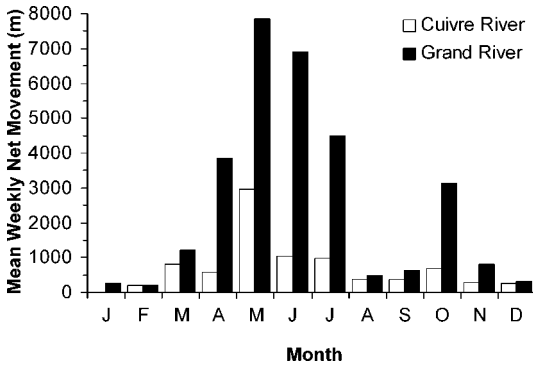


FIGURE 2.—Composite mean weekly net movement by month for flathead catfish radio-tracked in the Grand River and the Cuivre River, Missouri. See Methods section for how mean weekly net movement values were determined. Grand River data were collected from July 2001 to June 2002, Cuivre River data from July 2002 to June 2003.

**Results**

Descriptions of the annual movement cycle are based on 21 of the 37 flathead catfish implanted in the Grand River basin. Ten individuals were harvested by anglers within 1 year of implantation, and six fish were not relocated often enough to discern movement patterns. In the Cuivre River, 23 of the 27 fish implanted were used to document patterns. Two individuals were harvested within the first year, one fish died within a week of implantation, and the remaining individual was not relocated often enough to discern movement patterns. Relocations per individual fish included for this analyses had mean values of 69 (range, 39–101) and 75 (range, 35–83) relocations per fish in the Grand River and Cuivre River, respectively. Individuals at the lower end of the range of re-

TABLE 2.—Summary of results from two-way analysis of variance for the absolute linear seasonal range of flathead catfish in the Grand River and the Cuivre River. Seasonal period values were log<sub>10</sub> transformed before analysis to achieve normality; untransformed means and ranges are presented in Table 1. When analysis of variance showed a significant difference for a main effect (*P* < 0.05), Tukey's honestly significant difference (HSD) test was performed. Different lowercase letters indicate significant difference (*P* < 0.05) for class levels of the main effect.

Main effect class level	<i>F</i>	df	<i>P</i>	Tukey's HSD
Period	34.41	1, 109	0.0001	
Prespawn–spawn				x
Summer–fall				y
Overwintering				z
River	8.24	2, 109	0.0049	
Grand River				x
Cuivre River				y
Period × river	0.01	2, 109	0.9913	

locations for the annual cycle were those that spent the majority of their annual cycle in the Missouri River or Mississippi River.

Flathead catfish showed similar patterns of monthly movement activity, as evidenced by the mean weekly net movement in both watersheds (Figure 2), although net movements were greater in the Grand River basin.

When water temperatures rose above 10°C in mid-March, fish in both watersheds began to leave overwintering areas and migrated toward areas that would be used during the prespawn/spawning period. The prespawn/spawning period, from mid-April to mid-July, was characterized by increased movement. Movements in both watersheds were greater in seasonal ranges (Table 1) than in any other seasonal period (two-way ANOVA,  $\alpha$  < 0.05; Table 2). Even though the distances over

TABLE 1.—Descriptive statistics for annual movement of flathead catfish. Fish were radio-tracked from late June–early July 2001 through June 2002 in the Grand River basin (G) and from early July 2002 through June 2003 in the Cuivre River basin (C). Only fish that survived through the period were used in calculations. See Figure 5 for calendar time frames for seasonal periods. Ranges of those fish that spent the summer–fall period in the Missouri River and the Mississippi River and those that overwintered in the Mississippi River were not included because of limited data for those locations and periods. Directed movements were defined as instances when fish moved in one direction through successive relocations during migration periods or spates.

Variable	Mean		Median		Min.		Max.	
	G	C	G	C	G	C	G	C
Annual range (km)	63.4	22.5	53.7	26.3	16.8	1.5	187.7	46.4
Prespawn–spawning period range (km)	52.8	19.6	40.4	21.5	0.9	1.0	161.8	41.6
Summer–fall restricted movement period range (km)	12.7	6.3	7.8	2.4	0.8	0.2	50.4	29.6
Overwintering restricted movement period range (km)	4.1	3.0	5.1	0.7	0.1	0.1	12.1	25.3
Distance between overwintering area and summer–fall area (km)	22.2	7.0	16.2	3.5	9.2	0.0	44.6	26.1
Directed movement–migration rate (km/day)	4.2	6.2	2.6	3.3	0.2	0.8	24.1	26.9

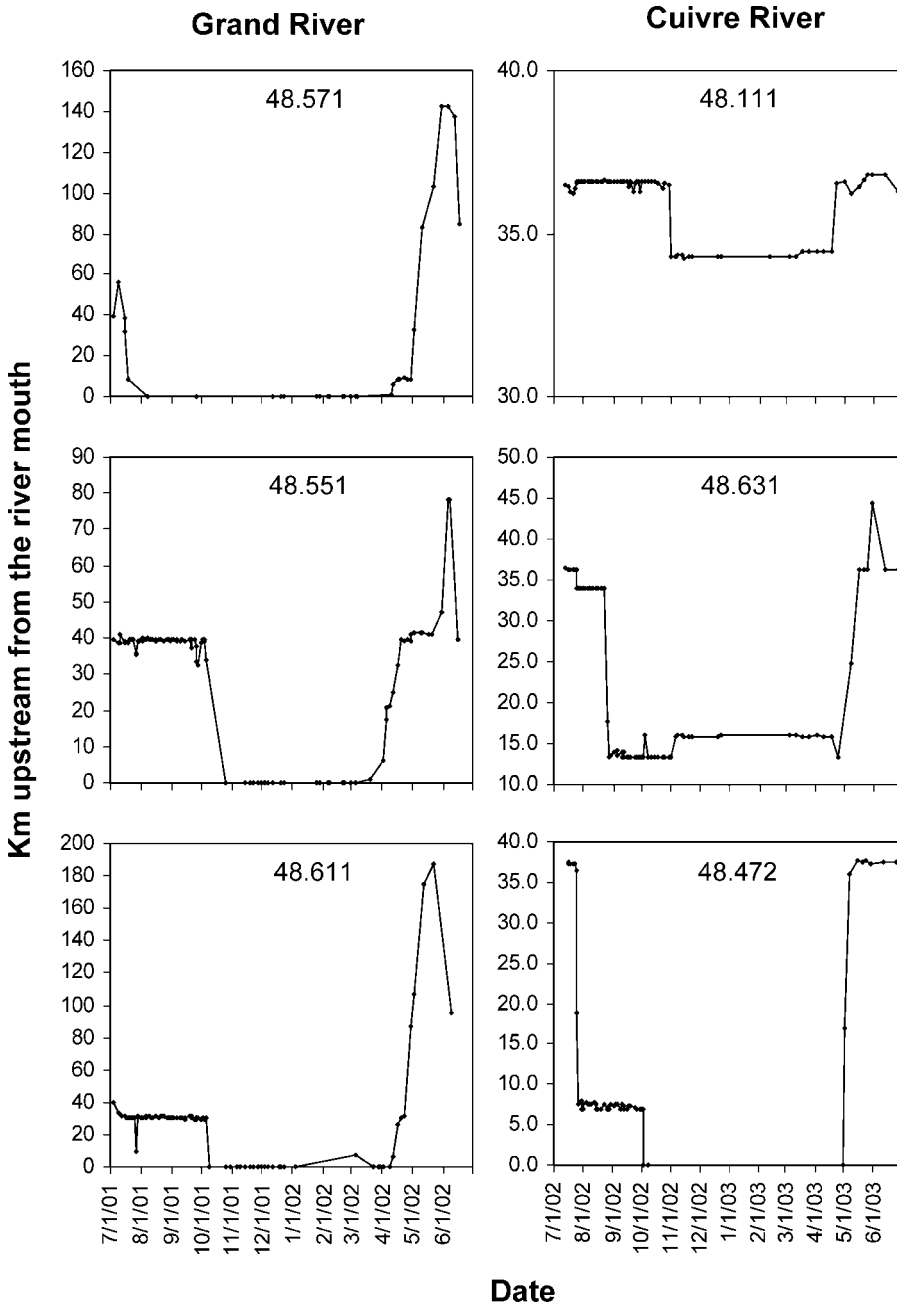


FIGURE 3.—Examples of interindividual variation in annual movement patterns from individual flathead catfish relocated in the Grand River and Cuivre River basins. During periods when fish left the Grand River and entered the Missouri River, relocations are represented by a marker at 0 km. Note: y-axis scales vary among panels.

which fish ranged were greater in the Grand River basin during the prespawn/spawning period, overall daily directed movement rates were similar (Table 1) in both watersheds. Individual fish moved upstream and downstream during the prespawn/

spawning period, although the general trend was upstream in both watersheds (Figure 3). Beginning in mid-July, fish made movements toward areas where they spent the summer/fall period, which is characterized by restricted movement. For some

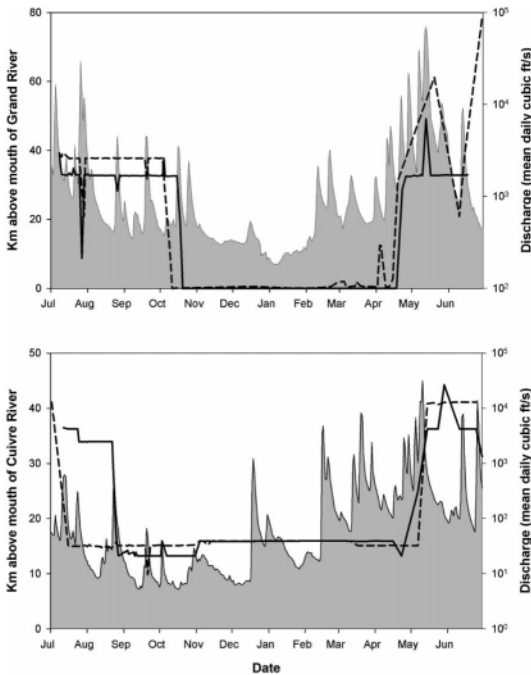


FIGURE 4.—Relationship between spates and movements through an annual cycle illustrated by two flathead catfish (solid and dashed lines) relocated in the Grand River basin (top panel) and the Cuivre River basin (bottom panel). Gray-shaded area denotes mean daily discharge recorded at U.S. Geological Survey stream gauge 06902000 near Sumner, Missouri, for the Grand River and at gauge 05514500 near Troy, Missouri, for the Cuivre River. Note: Date ( $x$ -axis) is 2001–2002 for the Grand River and 2002–2003 for the Cuivre River.

fish this migration was short—they remained in the main-stem Grand River or the main-stem Cuivre River—whereas other fish migrated longer distances back to the Missouri River or the Mississippi River (Figure 3).

The summer/fall period of restricted movement lasted from late July until mid-October. During this period, fish had lower weekly net movement (Figure 2) and a reduced range relative to that in the prespawn/spawn period (Table 1). Movement behavior of flathead catfish during this period was linked to high-use areas, as fish frequented particular habitat features such as log complexes and clay points. Spatially, the tagged population was at its most dispersed during this period in both watersheds, although some individuals remained in the same pool with other tagged fish (Vokoun 2003). During large spates associated with late-summer thunderstorms, some individuals moved long distances (>5 km; Figure 4), although others

did not. In the Grand River, all fish returned to their previous high-use areas after a spate-related movement. However, not all fish in the Cuivre River returned; those that did not then established a new high-use area (e.g., 48.631; Figure 3).

In late October, fish began migrating toward overwintering areas. The overwintering period lasted from mid-November to mid-March. During this time, linear river movement was at its lowest (Table 1). Fish aggregated at wintering sites and were often relocated in what appeared to be the same location (telemetry accuracy limited confidence in the exact relocations). Eight individuals overwintered in the same pool in the Cuivre River, and seven tagged fish overwintered together in the mouth of the Grand River. All documented fall migration in the Grand River basin was downstream in direction, although some fish in the Cuivre River moved upstream (e.g., 48.631; Figure 3).

Within the three-period annual cycle framework, individual fish displayed at least three variant pathways through an annual cycle (Figure 5). Some individuals entered the Grand River and Cuivre River watersheds during the prespawn/spawning period only and later returned to the Missouri River or the Mississippi River. These fish then spent the summer/fall period and the overwintering period in the big rivers, reentering the Grand River and the Cuivre River watersheds the following spring. Other individuals entered the Grand River and the Cuivre River watersheds for the prespawn/spawning period and remained there for the summer/fall period but returned to the big rivers to overwinter. In the Grand River, all individuals moved downstream (9–45 km) to the Missouri River and overwintered. However, some individuals in the Cuivre River aggregated in main-stem overwintering pools, while others migrated to the Mississippi River to overwinter.

## Discussion

The flathead catfish we radiotracked in two interior watersheds in Missouri did not conform to previous literature accounts of nonmigratory populations (Jackson 1999). That flathead catfish were migratory, and displayed variation within and between watersheds, was unexpected. Perhaps flathead catfish populations at more southern latitudes do not migrate, a result of the milder seasons there. Smallmouth bass *Micropterus dolomieu* in the Ozarks of southern Missouri displayed primarily restricted movement (Todd and Rabeni 1989); however, a northern population migrated as far as

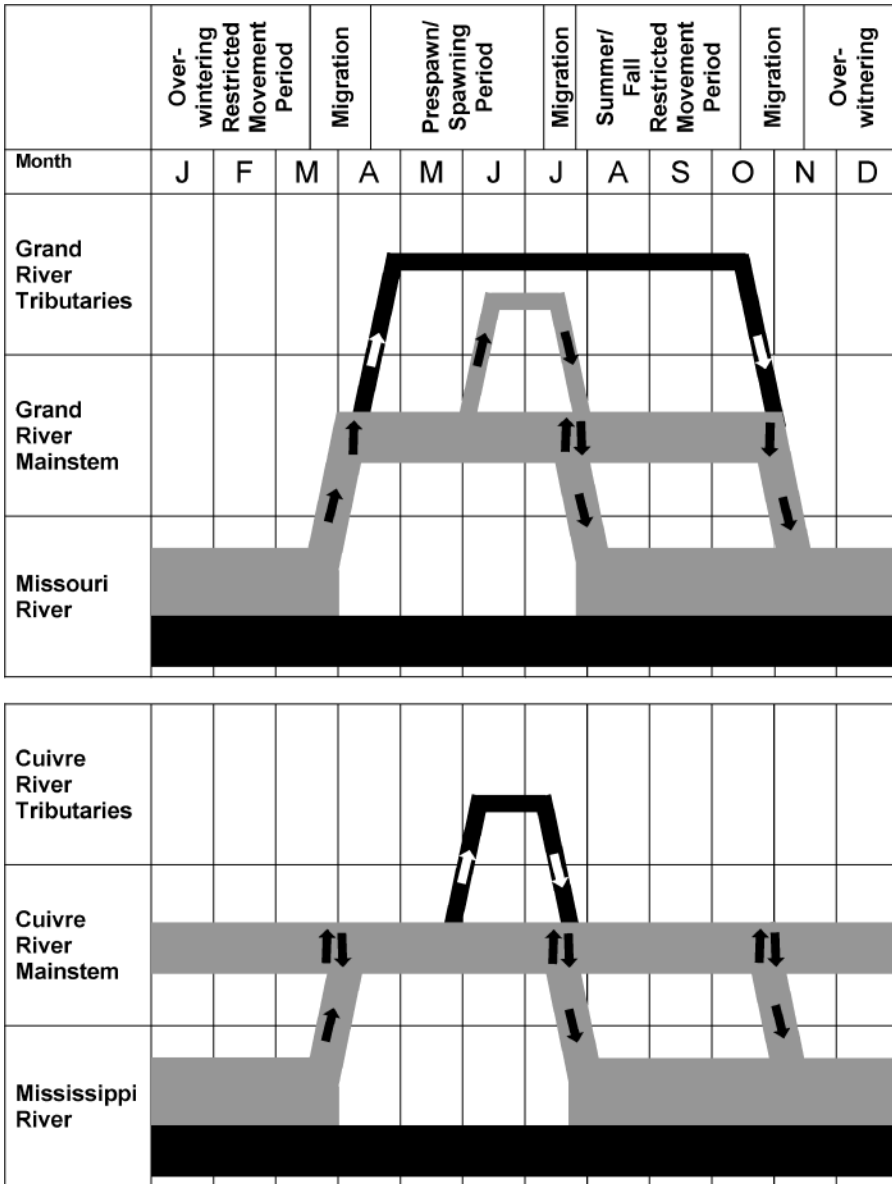


FIGURE 5.—Spatial pathways used to complete an annual cycle by radio-tracked flathead catfish in the Grand River and Cuivre River watersheds, Missouri, shown in gray. Hypothesized additional pathways supported by catch data and other recent research, but not documented by our radiotelemetry, are presented in black. Arrows denote the direction of the migrations that were documented by radiotelemetry.

87 km downstream to overwintering pools in the Embarras–Wolf River system in Wisconsin (Langhurst and Schoenike 1990). The limited availability of deep pools in the Embarras River was hypothesized to explain the migration.

Two tracking studies of flathead catfish were published while we were making our data collection. The first studied an introduced population of flathead

catfish in North Carolina and documented extremely mobile individuals that migrated to and from spawning areas (Kwak et al. 2004); the second study, in Michigan, found that fish also made seasonal movements to spawn and overwinter, although the distances traveled (<4 km; Daugherty 2004) were much less than those in our study and those reported in North Carolina (range, 1.4 to 45.9 km).

The within-watershed variation in migratory patterns we documented in Missouri was unique for flathead catfish studies to date but has also been found in other fish species. Rainbow trout *Oncorhynchus mykiss* were described as having different life history ecotypes, in that some of the different migratory patterns within a southwestern Alaska watershed separated fish during reproduction (Meka et al. 2003). Similarly, flathead catfish are presumed to spawn in the Missouri River and the Mississippi River, according to the catches there by commercial fishers and researchers (Travnicek 2004); these large-river spawners may represent an ecotype reproductively separated from the migratory fish that entered and reproduced in the Grand River and the Cuivre River watersheds.

Some authors have not considered potamodromous seasonal movements within watersheds as "true" migrations and refer to nonsalmonids collectively as "nonmigratory fishes" (Lucas and Baras 2001). In their recent review of freshwater fish migration, Lucas and Baras (2001:13) defined fish migration as "a strategy of adaptive value, involving movement of part or all of a population in time between discrete sites . . . usually but not necessarily involving predictability or synchronicity in time, since interindividual variation is a fundamental component of populations." We observed interindividual variation in the spatial pathways that flathead catfish used to complete the annual cycle. When fish move both upstream and downstream to reach overwintering habitats, as occurred in our study, one must acknowledge that the familiar diadromous-based concept of migration may be inappropriate for understanding potamodromous species.

In addition to the spatial variation observed, adult flathead catfish in the Grand River seemed to migrate individually during a seasonal period (e.g., mid-October to mid-November), in contrast to fish in the Cuivre River, which migrated in a more synchronous manner, timed with spates within the seasonal period. Radio-tracked fish in North Carolina and Michigan were not relocated often enough to assess independent or synchronous migrations (Kwak et al. 2004; Daugherty 2004; respectively), although the fish did migrate within a defined seasonal period, which is similar to our findings. Some evidence of spate-related movements were documented in North Carolina but were not reported in the Michigan study. Spates were shorter in the smaller Cuivre River basin, and certain riffles probably presented barriers to movement. Some fish in the Cuivre River did not return

to their previous high-use areas after a spate but instead established a new high-use area downstream nearer to the overwintering pools. This may be an example of a local adaptation or strategy that was not needed in the Grand River basin, where barriers to movement were rare and fish had reliable seasonal access to their overwintering sites in the Missouri River.

The variation in spatial pathways through which individual fish completed the annual cycle was surprising in scope. Four fish in the Cuivre River completed the annual cycle while spending 90% of the year in the same stream pool (a pool to which other fish also migrated for overwintering). The fish left only during the spawn and moved to the nearest location frequented by other fish during the broader prespawn/spawning period. Thus, specific stream pools in the Cuivre River offered both overwintering and favorable growth and feeding habitat but probably lacked suitable spawning habitat. Conversely, some pools provided spawning habitat and were used for the summer/fall period as growth and feeding habitat but were not used for overwintering. Still other fish entered the Cuivre River only during the prespawn/spawning period, returning to the Mississippi River for the remainder of the annual cycle. Similar spatial variation related to specific habitat features such as suitable wintering habitat was reported in Alaskan rainbow trout, where some fish migrated to and from two lakes on separate tributaries, while other fish made migrations exclusively in the lotic portions of the watershed (Meka et al. 2003). Migration of stream fishes has been described through a conceptual dynamic landscape model of life history presented in a series of papers by Schlosser (1991, 1995) and Schlosser and Angermeier (1995). Within this landscape framework, stream fishes are predicted to move to and from refugia during harsh conditions, to and from spawning habitats, and through a mosaic of feeding habitats over the course of an individual's lifetime. The radio-tracked adult flathead catfish generally did these three things in a highly seasonal, relatively synchronous manner.

Using as a starting point Schlosser's dynamic landscape model of the life history of stream fishes, Fausch et al. (2002) suggested that these fish often move through a "riverscape" at an intermediate spatial scale ranging from 1 to 100 km in absolute length and possibly including different sizes of river segments for different life cycle purposes. The intermediate spatial scale (1–100 km absolute range) generally characterized the annual movements of

flathead catfish, even though habitats did not always exist in the same relative locations in both basins (i.e., overwintering sites), and movement distances appeared to vary in scale with basin size. This spatial scale has often been ignored by researchers and managers, who take samples at small sites that often are located throughout the extent of the watershed. By not sampling at the intermediate spatial scales (often even with the use of telemetry), biologists have tended to miss the importance, frequency, and complexity of movements exhibited by relatively common freshwater fishes (Lucas et al. 2000; Fausch et al. 2002). Central to the riverscape framework is the hypothesis that the intermediate scales encompass often-separated habitats necessary to the completion of important annual (and lifetime) events (Fausch et al. 2002). This scenario was supported for flathead catfish in the Missouri populations we studied and in North Carolina rivers (Kwak et al. 2004), but less so in the St. Joseph River population in Michigan (Daugherty 2004), which suggests that the spatial arrangement of suitable habitats is probably context-specific (*sensu* Schlosser 1995).

Finally, the variable migratory behavior found in the two populations of flathead catfish in Missouri probably represents adaptive strategies that will, we hope, become better understood with further investigation. Our use of 400-d transmitters did not allow evaluation of whether individual fish followed the same pathway in successive years. Better than average battery life in the radio-tracking of a limited number of fish revealed that 5 of 10 fish returned to the core area of their previous summer/fall period locations in the Grand River and 9 of 16 returned in the Cuivre River, suggesting that fidelity rates to particular pools may not be high. However, at a coarser spatial scale, 96% of fish that left the Grand River and the Cuivre River watersheds, either after the pre-spawn/spawning period or after the summer/fall restricted-movement period, returned to their respective watersheds the following spring. Regardless, longer term monitoring is needed to understand whether fidelity exists for annual cycle pathways. We suggest that the plasticity displayed by the species should be embraced by management strategies, given that variation inherently strengthens the viability of populations (Northcote 1992). Reproductive success or overwintering survival is probably greater in particular locations within a given year (e.g., a tributary creek, the main-stem river, or the Missouri and Mississippi rivers), suggesting that abundances would benefit from long-

term maintenance of habitat quality and connectedness through time. Flathead catfish can be highly exploited locally. The Grand River radio-tagged population experienced 41% mortality to anglers in a 2-year period after implantation, whereas those in the Cuivre River experienced 11% mortality. Many of the fish were harvested in the Missouri River tens of kilometers from the Grand River reaches they used for spawning, feeding, and growth. Maximum directed movement rates of approximately 25 km/d were documented. This information suggests the utility of a larger scale for management than has been proposed. The quality of stream habitats, including the conditions for reproduction, growth, and overwintering, contribute to the fishery at distant locations. Further, the differences found among drainages existing at the same latitude but differing in size and habitat characteristics suggest that fisheries biologists should investigate particular watersheds at the intermediate scale of tens of kilometers to more effectively understand and manage flathead catfish populations in a long-term life history context.

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#### References

- Dames, H. R., T. G. Coon, and J. W. Robinson. 1989. Movements of channel and flathead catfish between the Missouri River and a tributary, Perche Creek. *Transactions of the American Fisheries Society* 118: 670–679.
- Dames, H. R., and 10 coauthors. 2003. Managing Missouri's catfish, a statewide catfish management plan, Quality Catfish Committee completion report. Missouri Department of Conservation, Jefferson City.
- Daugherty, D. J. 2004. Stock characteristics, movement patterns, and habitat use of flathead catfish in the lower St. Joseph River, Michigan. Master's thesis. Purdue University, West Lafayette, Indiana.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the

- gap between research and conservation of stream fishes. *Bioscience* 52:483–498.
- Funk, J. L. 1957. Movement of stream fishes in Missouri. *Transactions of the American Fisheries Society* 85:39–57.
- Gerking, S. D. 1950. Stability of a stream fish population. *Journal of Wildlife Management* 14:193–202.
- Gerking, S. D. 1953. Evidence for the concepts of home range and territory in stream fishes. *Ecology* 34:347–365.
- Gerking, S. D. 1959. The restricted movement of fish populations. *Biological Reviews* 34:221–242.
- Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51:2626–2637.
- Grace, T. B. 1985. The status and distribution of commercial and forage fish in the Missouri River and their utilization of selected habitats. Missouri Department of Conservation, National Marine Fisheries Service Program 2-363-R, Project 4, Job 3. Jefferson City.
- Hebrank, A. W. 1989. Geologic natural features classification system for Missouri. *Natural Areas Journal* 9:106–116.
- Jackson, D. C. 1999. Flathead catfish: biology, fisheries, and management. Pages 23–35 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. *Catfish 2000: proceedings of the international ictalurid symposium*. American Fisheries Society, Symposium 24, Bethesda, Maryland.
- Knighton, D. 1998. Fluvial forms and processes a new perspective. Arnold, London.
- Kwak, T. J., W. E. Pine, D. S. Waters, J. A. Rice, J. E. Hightower, and R. L. Noble. 2004. Population dynamics and ecology of introduced flathead catfish. U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit and Department of Zoology, North Carolina State University, Federal Aid in Sport Fish Restoration, Project F-68, Study 1, Phase 1, Final Report. Raleigh.
- Langhurst, R. W., and D. L. Schoenike. 1990. Seasonal migration of smallmouth bass in the Embarras and Wolf Rivers, Wisconsin. *North American Journal of Fisheries Management* 10:224–227.
- Lucas, M. C., and E. Baras. 2001. *Migration of freshwater fishes*. Blackwell Scientific Publications, Oxford, UK.
- Lucas, M. C., T. Mercer, G. Peirson, and P. A. Frear. 2000. Seasonal movements of coarse fish in lowland rivers and their relevance to fisheries management. Pages 87–100 in I. G. Cowx, editor. *Management and ecology of river fisheries*. Fishing News Books, Blackwell Scientific Publications, Oxford, UK.
- Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. *Transactions of the American Fisheries Society* 132:717–732.
- Montgomery, D. R., and J. M. Buffington. 1993. Channel classification, prediction of channel response, and assessment of channel condition. Washington State Department of Natural Resources, Timber/Fish/Wildlife Agreement, Report TFW-SH10-93-002. Olympia.
- Northcote, T. G. 1992. Migration and residency in stream salmonids—some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research* 67:5–17.
- Robinson, J. W. 1977. The utilization of dikes by certain fishes in the Missouri River. Missouri Department of Conservation, Federal Aid in Sport Fish Restoration, Project 2.199R. Jefferson City.
- Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704–712.
- Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* 303:71–81.
- Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes in lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Neilson, editor. *Evolution and the aquatic ecosystem: defining unique units in population conservation*. American Fisheries Society Symposium 17, Bethesda, Maryland.
- Schroeder, W. A. 1982. Pre-settlement prairie of Missouri. Missouri Department of Conservation, Natural History Series 2, Jefferson City, Missouri.
- Skains, J. A., and D. C. Jackson. 1995. Linear ranges of large flathead catfish in two Mississippi streams. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 47(1993):539–546.
- Stauffer, K. W., R. C. Binder, B. C. Chapman, and B. D. Koenen. 1996. Population characteristics and sampling methods of flathead catfish *Pylodictis olivaris* in the Minnesota River. Minnesota Department of Natural Resources, Division of Fish and Wildlife, Section of Fisheries, Federal Aid in Sport Fish Restoration, Project F-29-R-14, Study IV, Job 389, Final Report. St. Paul.
- Todd, B. L., and C. F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. *Transactions of the American Fisheries Society* 118:229–242.
- Travnicek, V. H. 2004. Movement of flathead catfish in the Missouri River: examining opportunities for managing river segments for different fishery goals. *Fisheries Management and Ecology* 11:89–96.
- Vokoun, J. C. 2003. Movement and habitat use of flathead catfish (*Pylodictis olivaris*) in two Missouri interior streams. Doctoral dissertation. University of Missouri, Columbia.